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Extinction patterns among bivalves in South China during the Permian–Triassic crisis

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ABSTRACT

Late Permian Changhsingian bivalves in South China are very abundant and diverse in nearshore, inner shelf, outer shelf, and deep basin facies. All reported data of both bivalve genera and species from the Permian–Triassic boundary strata of South China have been systematically collected and studied for understanding the evolutionary process of various bivalve groups in different environments through the great Permian–Triassic transition. At the genus level, bivalves show an extinction rate of 50% in the first phase of the Permian–Triassic crisis, though only 9.1% in the second phase. There appears to be no selection of extinction in life-style, feeding type or habitat among bivalves from South China through the crisis. There is no significant difference in the extinction rates between epifaunal and infaunal bivalve genera in all environments. Suspension feeders showed moderate extinction rates, while no deposit feeders went extinct at the genus level. In addition, infaunal bivalves were not at more risk of extinction than epifaunal forms. A combination of ocean anoxia and high seawater temperatures might have contributed to the mass extinction among bivalves during the Permian–Triassic crisis.

1. Introduction

The end-Permian mass extinction was the largest biotic catastrophe in the Phanerozoic (Raup, 1979; Alroy et al., 2008), but the patterns of extinction among different groups have been controversial. Fossil data from South China have been interpreted as a single phase of extinction (Jin et al., 2000; Shen et al., 2011) or a two or multi-phased event (Xie et al., 2005; Chen et al., 2009; Song et al., 2009, 2013; Yin et al., 2012). Many taxonomic groups, such as brachiopods (Chen et al., 2005a,b, 2006, 2011), foraminifers (Song et al., 2009), conodonts (Jiang et al., 2007), and bivalves (Fang, 2004), seem to fall into a two-phase pattern of mass extinction during the Permian–Triassic transition. The mass extinction also resulted in an important transition of marine ecosystem structures from the brachiopod-dominated Paleozoic Fauna to the mollusk-dominated Modern Fauna (Sepkoski, 1981; Benton, 2004; Fraiser and Bottjer, 2007; Chen et al., 2010). A variety of causes for this switch have been proposed, including the sharp demise of brachiopods, more efficient metabolic rates of bivalves, bivalve preference to nearshore settings, or physiological characteristics of mollusks (e.g., Steele-Petroric, 1979; Gould and Calloway, 1980; Thayer, 1985, 1986; Law and Taylor, 1991; Fraiser and Bottjer, 2007).

Early studies have suggested that bivalve diversity was only moderately affected by Permian–Triassic events (Nakazawa and Runnegar, 1973; Yin, 1985; Yang et al., 1987; Li, 1995), based mainly on taxonomic diversity at the family and genus levels, but these studies lacked an examination of the ecology of bivalves (Li, 1995; Fang, 2004; Clapham and Payne, 2011). This paper aims to probe bivalve evolution through the Permian–Triassic transition in both taxonomy and ecology on the basis of fossil records from South China.

2. Geological setting

As it was located in the low-latitude eastern Tethyan archipelago, South China contains continuous Permian–Triassic stratigraphic sequences with sedimentary settings from nearshore to deep basin (Fig. 1) (Feng et al., 1997; Tong and Yin, 2002). Abundant Changhsingian to Smithian bivalve fossil records enabled us to analyze the extinction pattern during the Permian–Triassic crisis. In this study, four sedimentary facies are distinguished in South China, i.e. nearshore, inner shelf, outer shelf, and deep basin facies (Fig. 1; Appendix 1, 2). Most of these facies can be recognized in the Upper Permian and Lower Triassic strata, although the facies had different spatial distributions and extents through the time (Feng et al., 1997).

The nearshore facies is characterized by marine and terrestrial mudstone, siltstone, sandstone, and coal beds of the Xuanwei and Kayitou Formations. This facies occurred mainly in the marginal areas of the Kangdian Old-Land such as eastern Yunnan, western Guizhou and southern Sichuan, and contains abundant brachiopods, bivalves, gastropods, ostracods, and plant fossils. The inner shelf facies is characterized by alternations of marine mudstone, siltstone, sandstone and muddy limestone, and occurred mainly in central Guizhou, e.g., Feixianguan

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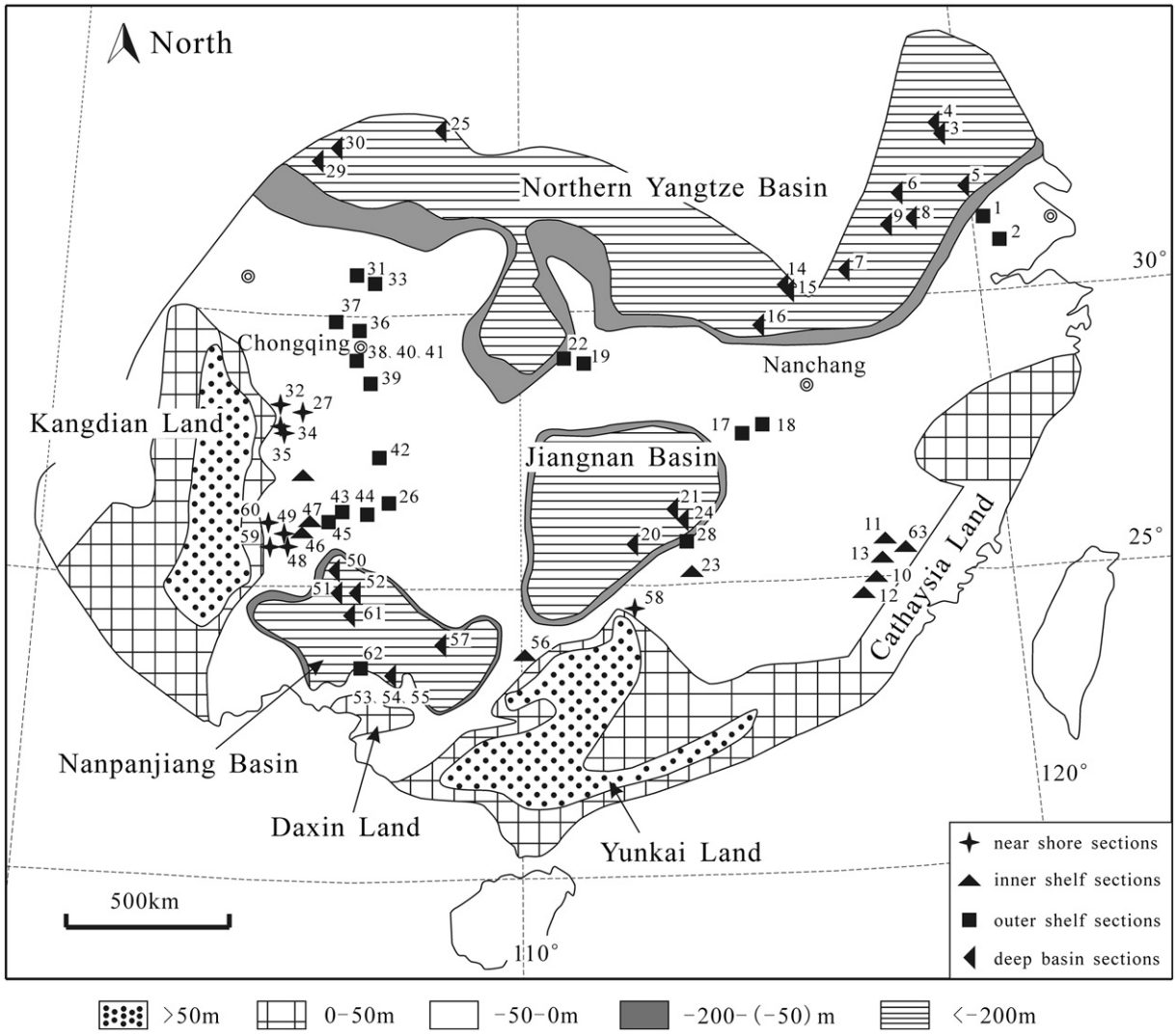

Fig. 1. Permian–Triassic paleogeographical configuration of South China showing sampling localities and paleogeographical settings of the bivalves. Section codes in Appendix 3. Base map modified after Wang and Jin (2000).

Formation, and western Fujian, e.g., Xikou Formation. This facies yields diverse brachiopods, ammonoids, bivalves and gastropods and rare foraminifers. The outer shelf facies includes carbonate platform and ramp settings, and is represented by various limestones such as the Changxing, Yelang and Jialingjiang formations, while the deep basin facies is characterized by shale, siltstone, cherty shale, and cherty siltstone, interbedded with thin-bedded limestone, i.e. Dalong, Linhao, Daye, Luolou and Yinkeng formations.

3. Materials and methods

A species-level bivalve database has been compiled from the primary literature with detailed biostratigraphic descriptions (Appendix 3). The details dealing with the fossil bivalves, such as lithostratigraphy, chronostratigraphy, sedimentology, taxonomy and paleoecology, are filtered and recorded in the database for most of the reported Late Permian Changhsingian to Early Triassic Smithian bivalve fossils in South China. Over 700 species in 105 genera have been analyzed from 63 Changhsingian to Smithian sections (see references in Appendix 3). The age of each species is given in relation to its occurrence relative to the two extinction events during the Permian–Triassic crisis (Fig. 2). The lifestyles of bivalves are subdivided into epifaunal attached, including epi-byssate and epi-cemented, epifaunal motile, including facultative mobile and pseudoplankton, semi-infaunal, shallow infaunal and deep infaunal habits. For comparison between infaunal and epifaunal bivalves, we assigned the epifaunal attached and epifaunal motile modes of life to epifaunal bivalves, while infaunal bivalves were assigned as semi-infaunal, shallow infaunal and deep infaunal. The feeding types of bivalves were divided into deposit feeder and suspension feeder. However, the deposit-feeders in our dataset all belong to Orders Nuculoida, Nuculanida, and Solemyoida. Thus, the deposit feeders are a minority compared to suspension feeders, which means that the ecological selectivity of deposit feeders versus suspension feeders might seem not very significant.

As species richness is strongly influenced by sample size, a rarefaction analysis typically was employed to test the sample efficiency/bias in community analysis (e.g., He et al., 2007; Chen et al., 2010) using the paleontological statistical analysis package PAST (Hammer et al., 2001). Here, the rarefaction analysis of genus richness against the number of sections, which could reflect expected taxonomic richness in one specific period (Shen et al., 2011; Song et al., 2013), is used in this study (Fig. 3).

Genus richness, extinction rates, and origination rates in four different environmental settings are presented in Table 1 and Fig. 4. The data for genus richness, extinction rates, and origination rates of different lifestyles of bivalves inhabiting various facies are shown in Table 2,